Relationships of Certain Holarctic Shrews, Genus Sorex

By Robert S. Hoffmann

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A number of authors in recent years have proposed that each of several species of *Sorex* has a Holarctic distribution. KUZYAKIN (in BOBRINSKII et al., 1944) while reducing the number of recognized Russian species to six, suggested that the Palearctic *S. araneus* was closely related to *S. tundrensis* and *S. arcticus* of the Nearctic; CHAWORTH-MUSTERS (in ELLERMAN and MORRISON-SCOTT 1951) regarded certain of these Palearctic populations as conspecific with *S. tundrensis;* RAUSCH (1953) considered *S. tundrensis* from Alaska as conspecific with *S. arcticus* from further east, but cautioned that relationships between *araneus, tundrensis,* and *arcticus* remained to be worked out; he later concluded (1963), following SHVARTS (1959), that *S. arcticus,* but not *S. araneus,* was Holarctic.

BOBRINSKII et al. (op. cit.) also suggested that *S. mirabilis* from eastern Siberia was conspecific with *S. pacificus* from western North America, and was followed by ELLERMAN and MORRISON-SCOTT (op. cit.). FINDLEY (1955) who placed *pacificus* in *S. vagrans*, made no comment on *S. mirabilis*.

VAN DEN BRINK (1953, 1967) regarded the Old World S. caecutiens as conspecific with S. cinereus of the New World, and also followed the previously cited authors in regarding S. araneus (including tundrensis and arcticus) and S. pacificus (including mirabilis) as Holarctic species. Finally, VAN DEN BRINK (1953), and SKAREN (1964) suggested that the Palearctic S. unguiculatus and S. sinalis (listed as subspecies of araneus by ELLERMAN and MORRISON-SCOTT, op. cit.) were conspecific with S. obscurus (previously united with S. vagrans by FINDLEY, op. cit.) and also comprised a Holarctic species.

If these various proposals were accepted, three taxa, as follows, would have to be considered Holarctic species:

- 1. Sorex araneus Linnaeus, 1758, consisting of S. araneus (sensu stricto); S. tundrensis Merriam, 1900; and S. arcticus Kerr, 1792.
- 2. Sorex caecutiens Laxmann, 1788, consisting of S. caecutiens (sensu stricto); S. cinereus Kerr, 1792; S. prebli Jackson, 1922; and S. lyelli Merriam, 1902.
- 3. Sorex vagrans Baird, 1857, consisting of S. obscurus Merriam, 1891; S. pacificus Coues, 1877; S. yaquinae Jackson, 1918; S. mirabilis Ognev, 1937; S. unguiculatus Dobson, 1890; and S. sinalis Thomas, 1912; as well as S. vagrans (sensu stricto).

It is clear from an examination of the pertinent literature that the key to the problem of Holarctic relationships in *Sorex* resides in, first, the correct interpretation of relationships among shrew taxa in the Palearctic, and especially eastern Siberia, and second, an understanding of the relationships between taxa of eastern Siberia and western North America, on either side of the presently-existing barrier, Bering Strait. In recent years much has been accomplished by Russian mammalogists in clarifying the situation among overly-lumped taxa of Palearctic shrews, and it seems useful at this time to review and interpret this recent work for the benefit of European and American workers whose access to the Russian literature is limited. Supplementing this review are certain new data and new interpretations of the relationships of certain taxa in eastern Siberia and western North America.

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After this paper was in the editor's hands, an important new paper on Holarctic shrews arrived; "Novie dannie po sistematike nekotorikh vidov zemleroek (Soricidae) Palearktiki i Nearktiki", Acta Theriologica, 14 (3): 21–34, 1969, by BORIS YUDIN, who independently reached many of the same conclusions presented in the present paper.

The Sorex araneus - tundrensis - arcticus group

STROGANOV (1957) published a detailed study of the insectivores of Siberia, in which he divided the Sorex araneus group into five species in addition to the nominate species. According to him, Sorex asper was restricted to the Tyan Shan Mountains; S. unguiculatus to the Amur-Ussuri River region and Kamchatka, in the Soviet Far East; Sorex daphaenodon and S. vir were restricted to Siberia east of the Ob and Yenesei rivers; and S. arcticus was considered to range from eastern Siberia westward to the Ural Mountains. Sorex araneus proper was considered by him to occupy the western Palearctic, occuring eastward only as far as a line drawn from the Ob estuary to Lake Baikal. Ecological studies in central Siberia by YUDIN (1962) confirmed the sympatric existence of four species of the "araneus group" in this area.

GUREEV (in GROMOV et al. 1963) followed STROGANOV in most respects, but recognized an additional species of the "araneus group" as distinct, S. raddei, in the Caucasus Mountains. KUZYAKIN (in BOBRINSII et al. 1965) in the revised edition of their work, while agreeing to the separation of S. unguiculatus and S. daphaenodon, did not follow StrogANOV and GUREEV in recognizing as species arcticus, asper, raddei or vir; FLINT et al. (1965) did likewise. DOLGOV (1966, 1967), the most recent student of Palearctic Sorex, not only admitted all of the species previously raised to this rank by STROGANOV and GUREEV, but split off from what remained of S. araneus two more species. DOLGOV considered Sorex caucasicus, like S. raddei, to be restricted to the Caucasus Mountains; while S. centralis was considered to have a broad trans-Palearctic range, in the taiga zone. SIIVONEN (1965) thought that the species to which DOLGOW applied the name S. centralis should bear the name S. isodon, and that the specimens on which the name S. centralis was based may belong to the S. caecutiens group. Finally, S. robaratus of the Altai Mountains may be a distinct species in the "araneus group" (YUDIN and BARSOVA 1967), and recent cytological studies of S. araneus in western Europe indicate that there are actually two sibling species there (Meylan 1964, 1965).

If S. centralis (or isodon) be admitted as a species, and recent studies of its chromosomes support this (HALKKA et al. 1970), then, according to DOLGOV and YUDIN, the central Siberian highlands between the Ob und Yenesei rivers are inhabited by five species of Sorex superficially so similar that they have in the past all been considered to belong to one species, Sorex araneus. Farther east, toward Bering Strait, at least four species still occur – arcticus, centralis (= isodon), daphaenodon, and vir. Of these only S. arcticus appears to be a Holarctic species, closely resembling S. arcticus tundrensis of northwestern North America (HOFFMANN and PETERSON 1967). If tundrensis should eventually prove specifically distinct from S. a. arcticus and other subspecies in North America (P. M. YOUNGMAN pers. comm.) then the Holarctic species (and its Siberian subspecies) will bear the name Sorex tundrensis.

The Sorex caecutiens - S. cinereus problem

STROGANOV (op. cit.) was the first to report the existence in Siberia of Sorex cinereus, a species previously regarded by most as Nearctic. As noted above, VAN DEN BRINK considered cinereus conspecific with S. caecutiens, forming a Holarctic species, but

this position is not tenable if *cinereus* and *caecutiens* are geographically sympatric in eastern Siberia. Additional support for the view that they are distinct species derives from their karvotypes; in North American S. cinereus 2n = 66 (MEYLAN 1968), and in S. caecutiens, 2n = 42 (SKAREN and HALKKA 1966, FREDGA 1968). Subsequent Soviet authors have either assigned the supposed cinereus specimens from Siberia to S. caecutiens (FLINT et al. 1965); to S. minutus (KUZYAKIN, in BOBRINSKII et al. 1965), or have not dealt with the problem (GUREEV, in GROMOV et al. 1963; DOLGOV 1966, 1967). HOFFMANN and PETERSON (1967) compared not only specimens of Siberian cinereus and caecutiens with Alaskan cinereus, but also with the insular populations of the Bering Sea, S. jacksoni (St. Lawrence Island), S. pribilofensis (St. Paul Island, Pribilofs), and the holotype and topotype of S. hyrdodromus (Unalaska Island). It was concluded that these three insular populations should be assigned to the cinereus group rather than the araneus-tundrensis-arcticus group to which they had been allocated by earlier authors. Sorex cinereus is thus a Holarctic species, extending from North America across the Bering Strait and several of its islands to eastern Siberia, where it is sympatric with the phenetically similar S. caecutiens and S. minutus (HOFFMANN and PETERSON op. cit.).

VAN DEN BRINK (1953) also regarded the Nearctic S. preblei and S. lyelli of the cinereus group as conspecific with S. caecutiens. There is, however, new evidence that S. preblei is distinct from, and sympatric with, S. cinereus in at least one area, western Montana (HOFFMANN et al. 1969).

Sorex mirabilis, S. pacificus and the presumed Rassenkreis in Sorex vagrans

KUZYAKIN'S original suggestion that *S. mirabilis* of the Amur-Ussuri River region of the Soviet Far East could not be separated from *S. pacificus* of the northwestern coast of the United States was rejected by STROGANOV (op. cit.). He was followed by GUREEV (in GROMOV et al. 1963), but KUZYAKIN reaffirmed his original opinion (in BOBRINSKII et al. 1965), while rejecting FINDLEY'S contention that *pacificus* should be considered a subspecies of *S. vagrans*. The name of the Ussuri giant shrew was thus *Sorex pacificus mirabilis*, as FLINT et al. (1965) agreed. DOLGOV (1966, 1967) instead followed STROGANOV, and subsequently HEPTNER and DOLGOV (1967) proposed a new subgenus, *Ognevia*, to accommodate what they believed to be important peculiarities

found in S. mirabilis. They state: "... the structure of the anterior upper incisor ... [differentiates] this species from all other species of the genus Sorex . . ." (translation mine). The structure in question is a well-developed medial tine (Zu-BETS) or cusp on the surface of the first upper incisor (inset, Fig. 1). This medial tine, although absent in S. pacificus) (inset, Fig. 2) is not restricted to S. mirabilis, as implied by

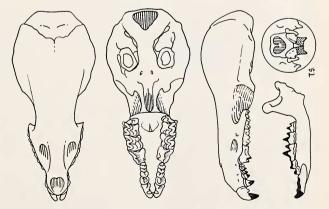


 Fig. 1. Sorex mirabilis, Ussuri giant shrew, Sudzuzhin Preserve,
 Primorsk region, U.S.S.R. Moscow State Univ., No. 51254,
 Q, X 4. Note medial tines or cusps on surface of upper incisors, as seen in frontal view (inset, lower right)

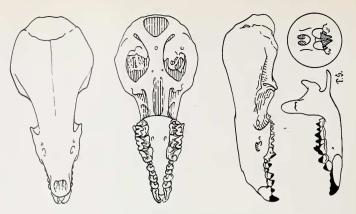


Fig. 2. Sorex pacificus, Pacific shrew, Crescent City, Del Norte County, California, U.S.A. Mus. Nat. Hist., Univ. Kansas, No. 14713, 3, X 4. Note absence of medial tine on surface of upper incisors (inset, lower right)

HEPTNER and DOLGOV. The tine attains significant development in the vagransobscurus group (Fig. 3) which FINDLEY (1955) considered to be a Rassenkreis of overlapping subspecies one of whose end members, S. v. vagrans, was sympatric with, but did not intergrade with, the members of the other end (S. v. pacificus, S. v. bairdi, etc.) in the northwestern United States. This interpretation was based on what was thought to be evidence of interbreeding between S. v. vagrans and S. v. obscurus in the Rocky Mountains. However, in at least one area of presumed intergradation, western Montana, re-analysis of larger samples, supported by qualitative differences in medial tine structure, indicate that gene flow between the larger, montane populations (S. obscurus as defined by JACKSON) and the smaller lowland populations (S. vagrans) in non-existent, or at most, slight (HENNINGS 1970).

Finally can S. unguicalatus and S. obscurus be considered conspecific, as VAN DEN BRINK and SKAREN did? SILVONEN (1965) pointed out that differences in the uni-

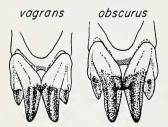


Fig. 3a (left). Sorex vagrans, vagrant shrew, Hamilton, Ravalli County, Montana, U.S.A. Dartmouth College Mus., No. 158-45-3030. X 15 - Fig. 3b (right). Sorex obscurus, dusky shrew, Beartooth Plateau, Park County, Wyoming, U.S.A. Univ. Montana Zool. Mus., No. 7186. X 15. Note differing position of secondary tines on medial incisor surface in the two species. From HENNINGS, 1970

cuspid teeth refutes this concept, and my comparison of specimens of the two taxa shows that there are also phenetic differences in pelage color, size, and tooth structure.

Thus, the species concepts of KUZYAKIN, FINDLEY, VAN DEN BRINK and SKAREN which if logically combined, would make Sorex vagrans a Holarctic species, are shown to be invalid. Among the proposed component populations, S. mirabilis and S. unguiculatus are restricted to the Asian coast of the Pacific Ocean, while S. pacificus is restricted to the North American side. The relationships between pacificus, obscurus, and vagrans obviously require further study, but I believe that present evidence is on the side of their being distinct species.

Are other taxa of Sorex Holarctic?

SILVONEN (1965) raises this question, and hints that some do. He goes on to suggest a major program to unravel the knotty questions of soricid taxonomy. As a

Mean and range for selected skull and body measurements of Sorex mirabilis and S. bendirii

		Sorex bendirii				
	Sorex mirabilis	albiventris	bendirii	pali	palmeri	
N	8	2—3	7	Oregon 9	California 6	
Condylobasal Length Palatal Length Maxillary Tooth Row Maxillary Breadth Mastoid Breadth Cranial Usight	$ \begin{array}{r} 10.03 \\ (9.6-10.3) \\ 8.49 \\ (8.2-8.6) \\ 6.66 \\ (6.4-7.0) \\ 10.49 \\ (10.1-10.8) \\ 6.06 \end{array} $	$\begin{array}{c} 8.47\\ (8.4-8.6)\\ 6.93\\ (6.8-7.1)\\ 11.05\\ (11.0-11.1)\\ 6.83\end{array}$	9.89 (9.5-10.1) 8.86 (8.2-9.2) 7.20 (6.9-7.5) 11.20 (10.5-11.9) 7.03	$ \begin{array}{r} 10.16 \\ (9.9-10.7) \\ 9.34 \\ (9.1-9.6) \\ 7.32 \\ (7.0-7.6) \\ 11.43 \\ (10.8-11.9) \\ 7.26 \end{array} $	9.68 (9.3-9.9) 8.95 (8.6-9.2) 6.80 (6.7-6.9) 10.82 (10.6-11.2) 6.62	
Height Interorbital Breadth Body Length Tail Length Hind Foot Length	$\begin{array}{c} (5.8-6.5) \\ 4.71 \\ (4.6-4.9) \\ 82.3 \\ (73-91) \\ 65.3 \\ (64-68) \\ 16.6 \\ (16-17.5) \end{array}$	$(6.7-7.0) \\ 4.2 \\ 85.0 \\ (81-91) \\ 70.7 \\ (62-79) \\ 19.3 \\ (19-20)$	$\begin{array}{c} (6.77.3) \\ 4.37 \\ (4.14.5) \\ 93.0 \\ (85100) \\ 73.0 \\ (6582) \\ 19.9 \\ (1920) \end{array}$	$\begin{array}{c} (7.0-7.5) \\ 4.34 \\ (4.1-4.6) \\ 93.3 \\ (88-97) \\ 74.9 \\ (67-82) \\ 20.7 \\ (19-22) \end{array}$	$\begin{array}{c} (6.3-6.9) \\ 4.27 \\ (4.1-4.5) \\ 82.2 \\ (75-85) \\ 68.7 \\ (61-73) \\ 20.3 \\ (19-22) \end{array}$	

preliminary contribution, I wish to suggest that the greatest similarities are not between S. pacificus and S. mirabilis, but rather between the latter and Sorex bendirii. Both are, in external measurements, the largest shrews in the genus. Both inhabit the forest floor and stream banks of mesic mixed coastal forests. Both are restricted to remnant stands of the old amphi-Beringian mesophytic forest whose connection across the Bering Strait area was severed in late Miocene (WOLFE and LEOPOLD 1967). Morphologically, both have well-developed secondary tines on the first upper incisors. Cranial measurements and proportions are compared in Table 1 and Figs. 1 und 4. Principal phenetic differences are color, and occurrence of the post-mandibular canal. Although both are essentially unicolored, S. mirabilis is paler - STROGANOV (op. cit.) describes it as near hair brown (RIDGEWAY 1912, Pl. XLVI). Sorex bendirii is, in contrast, much darker; also, most specimens lack a post-mandibular canal, whereas most specimens of mirabilis possess one (Table 2).

Table 2

Whether or not these phenetic similarities signify a distant phylogenetic relationship is totally uncertain at present. Certainly, each taxon is distinctive, and both have been placed in separate, monotypic subgenera. The lineage of the genus Sorex is known back to the late Oligocene in Europe and

Frequency	of occurence of	post-mandibular	foramen in Sorex
	mirabilis	and S. bendirii	

	Present	Absent
Sorex mirabilis	12	2
Sorex b. bendirii	2	12
Sorex b. palmeri, Oregon	2	16
Sorex b. palmeri, California	2	10

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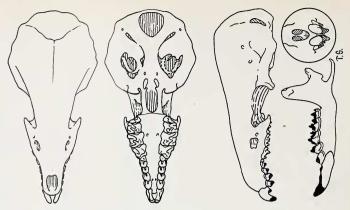


Fig. 4. Sorex bendirii, Pacific "water" shrew. Tillamook Co., Oregon, U.S.A. Mus. Vert. Zool., Univ. California, No. 81157, 3, X 4. Note small medial tines on surface of upper incisors (inset, lower right)

early Miocene in North America. Consequently, it is conceivable that an ancestral shrew occupying the mesophytic coastal forest around the North Pacific Basin was divided by climatic deterioration in late Miocene-early Pliocene and eventually gave rise to two specialized relict species populations on opposite sides of the Pacific Ocean. On the other hand, the phenetic similarities noted could well be the result of convergent evolution adapting two separate lineages of shrews to similar ecological niches in the two regions.

A tentative classification of the shrews discussed above, based on the views of the authors cited, as well as my own interpretations, is as follows. Group 1:

> Sorex araneus Linnaeus, 1758 Sorex arcticus Kerr, 1792 Sorex asper Thomas, 1914 Sorex caucasicus Satunin, 1913 Sorex centralis Thomas, 1911 Sorex daphaenodon Thomas, 1907 Sorex raddei Satunin, 1895 Sorex roboratus Hollister, 1913 Sorex unguiculatus Dobson, 1890 Sorex vir G. Allen, 1914

Group 2:

Sorex caecutiens Laxmann, 1788

Group 3:

Sorex mirabilis Ognev, 1937

Group 4:

Sorex bendirii Merriam, 1884

Group 5:

Sorex pacificus Coues, 1877 Sorex obscurus Merriam, 1891 Sorex vagrans Baird, 1857

Group 6:

Sorex cinereus Kerr, 1792 Sorex lyelli Merriam, 1902 Sorex preblei Jackson, 1922 Sorex pribilofensis Merriam, 1895

Of the species listed, only S. arcticus and S. cinereus are at present regarded as Holarctic. Further study of the genus is clearly needed, and will undoubtedly result in changes in this tentative classification.

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Summary

The systematics of taxa of shrews (Sorex) that have been considered by one or another author to belong to Holarctic species is reviewed. Of twenty species tentatively recognized, only two, S. arcticus and S. cinereus, are regarded as Holarctic, and proposals that S. caecutiens, S. pacificus, and S. unguiculatus are Holarctic are rejected.

Zusammenfassung

Die Systematik der Taxa der Spitzmäuse (Sorex), die von verschiedenen Autoren als holarcti-sche Arten angesehen werden, wurde nachgeprüft. Von 20 vorläufig bestimmten Arten können nur zwei, S. arcticus und S. cinereus, als holarctische Arten betrachtet werden. Der Vorschlag S. caecutiens, S. pacificus und S. unguiculatus seien holarctisch wird zurückgewiesen.

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Superfetation beim Virginia-Hirsch (Odocoileus virginianus Zimmermann 1780)?

Von Wolf Bartmann

Aus dem Zoologischen Garten Duisburg Direktor: Dr. W. Gewalt

Eingang des Ms. 1. 3. 1971

Es ist in der Zootierhaltung eine bekannte Tatsache, daß bereits trächtige Weibchen bei verschiedenen Tierarten bis unmittelbar vor dem Geburtstermin erneut oder gar öfters nachgedeckt werden können. Dabei kommt es in der Regel weder zu Störungen der Trächtigkeit, noch zu weiteren Befruchtungen, wenn dem neuerlichen Deckakt beim weiblichen Tier keine Ovulation vorausgeht oder folgt. Tritt aber tatsächlich Empfängnis bei einem schon tragenden Weibchen ein und entwickeln sich im Genitaltrakt gleichzeitig Eier von verschiedenen Ovulationszyklen, so bezeichnet man diese Form der Doppelträchtigkeit als Superfetation.

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